

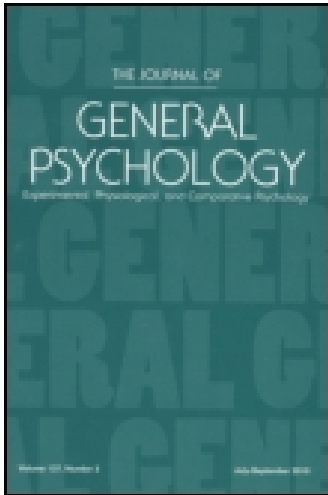
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T. Cunliffe Barnes^a & B. F. Skinner^a

^a Laboratory of General Physiology, Harvard University, USA

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THE PROGRESSIVE INCREASE IN THE GEOTROPIC RESPONSE OF THE ANT *APHAENOGASTER**

From the Laboratory of General Physiology, Harvard University

T. CUNLIFFE BARNES AND B. F. SKINNER

Although various tropisms [cf. (1)] of animals are now well known (with the possible exception of chemotropism) there are several categories of movements which still appear to be rather anomalous. Spontaneous and intermittent activity, tropism reversals, "random" movements and variations in the degree of tropistic response require extended investigation. In the present paper certain somewhat novel features in the geotropic response of the ant *Aphaenogaster* are described, and partially explained in terms quite compatible with the traditional "forced movement" philosophy. One of us¹ has recently reported that typical geotropic orientation may be secured with ants on an inclined plane. In the course of those enquiries unusual changes in the geotropic sensitivity of *Aphaenogaster fulva* were discovered.

All our work with *Aphaenogaster* was carried on in a dark room under dim red illumination, for these ants are greatly affected by light. In bright light we were able to obtain definite phototropic paths which are of interest in connection with the studies of Loeb and of Santschi on ants. The former (3, p. 109) stated that he never found true heliotropism in the workers and the latter (4, p. 384) claimed that the disturbance produced in the behavior of ants by reflecting the sun's rays upon them with a mirror was not phototropism.

We have used the same simple technique which was found suitable with *Crematogaster* and *Lasius*. The insect is lifted gently on a small square of paper to the center of an inclined plane and allowed to crawl away in any direction. The path is followed with a soft pencil upon a sheet of paper on which the ant may secure a firm foot-hold at any inclination. As with *Crematogaster* and *Lasius*,

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¹Barnes, T. C. *J. Gen. Psychol.*,

only the worker ants were used. Individual workers were studied over a wide range of angles of inclination (α) of the substratum, and others were tested at intervals for several days with a constant tilt of the plane. In both cases the θ angle of geotropic orientation, measured as deviations from a line parallel to the horizontal axis of the plane exhibited a progressive increase. The method of measuring the θ angle is given in Figure 3.

The rise in the gravity response may be seen in Figure 1 where the order in which the various records were taken is indicated on the curve. In this case the increase in the θ angle is opposed by using lower and lower inclinations. At each point the angle of orientation represents the average of 40 measurements on 20 trails each about 15 centimeters in length. The heightened geotropic response, especially obvious between points 2 and 4, was finally overcome by the markedly decreased gravitational component at 5. The time at

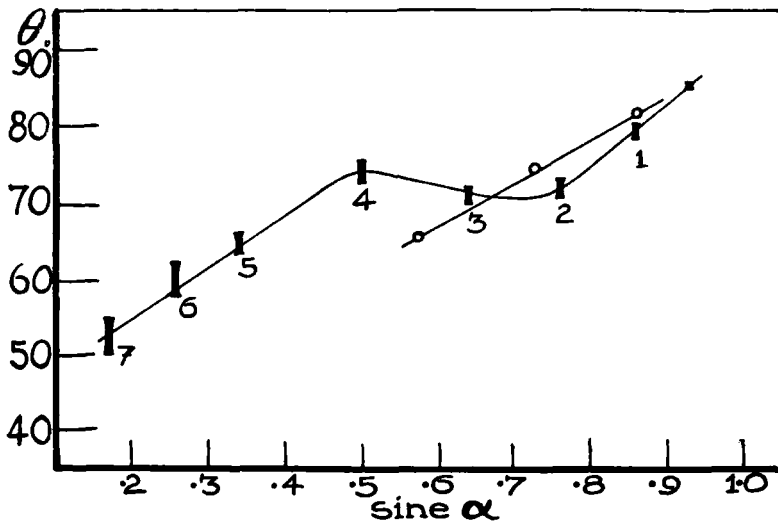


FIGURE 1

The intersection of the curve representing the geotropic orientation of *Aphaenogaster* at progressively lower angles and the line giving the response when the angle of inclination is progressively increased from low values. The numbers indicate the order in which the records were taken (vide Table 1). The bars are proportional to the probable errors. The line joining the dots gives the result of the ascending values of α for a second ant (vide Table 2).

TABLE 1

THE GEOTROPIC RESPONSE OF *Aphaenogaster* No. 1 TESTED AT VARIOUS TIMES
AND INCLINATIONS OF THE PLANE

$n = 40$. Positive Geotropism

Trial No.	α (degrees)	θ P.E. (degrees)	Time
1	60°	79.4° ± 1.12	Sept. 14, 4-4:25 P.M.
2	50°	72.0° ± 1.39	4:36-4:52
3	40°	71.0° ± 1.24	5:06-5:18
4	30°	74.3° ± 1.53	5:27-5:56
5	20°	64.7° ± 1.45	10:23-10:29
6	15°	60.0° ± 2.15	Sept. 15, 11:10-11:31 A.M.
7	10°	52.7° ± 2.40	11:57-12:02
8	70°	85.4° ± 0.56	Sept. 17, 10:51-11:03 A.M.

TABLE 2

THE GEOTROPIC RESPONSE OF *Aphaenogaster* No. 2 AT VARIOUS TIMES AND
INCLINATIONS (α) OF THE PLANE

$n = 40$. Negative Geotropism

Trial No.	α (degrees)	θ P.E. (degrees)	Time
1	35	65.6 ± 2.39	Sept. 18, 5:36 P.M.
			Sept. 19, 3:40 P.M.
2	45	74.4 ± 1.41	Sept. 19, 4-4:30 P.M.
3	60	81.4 ± 0.87	Sept. 24, 11:35 A.M.
			4:42 P.M.

which each of these records was taken is given in Table 1. When the procedure is reversed and the first angles taken are the lower ones, a curve is obtained which intersects the first (the line indicated by circles in Figure 1). In Table 2 is recorded the first test made at $\alpha = 35^\circ$, in which the θ angle is nearly 10 degrees lower than the (fourth) record in Table 1 at $\alpha = 30^\circ$.

The effect is perhaps most striking when records are obtained with an *Aphaenogaster* on a surface of constant inclination over a period of several days. The individual is taken from the colony and kept in a watch glass with moist blotting paper without food. Such an ant dies in four to eight days if not returned to the nest. Figure 2 presents the progressive rise in the θ angle of nearly 10 degrees at 50° inclination of the substratum. It seemed quite possible that this rise might be interpreted as a species of geotropic

"learning," and the following experiment was devised to throw light on the question. For a short time on each of three days an individual was permitted to crawl on a level surface for approximately the same distance as the usual inclined plane record and on the fourth day the geotropic orientation was tested on a 50° incline. For the following three days trails were secured again on the level and a final geotropic response was recorded at the 50° incline. The measurements represented graphically in Figure 4 lead one to suggest that the "training" under gravitational stimulation is not the chief factor involved in the progressive rise in θ , for after three days with brief exercise on a horizontal surface the value has arisen to 68.5°,

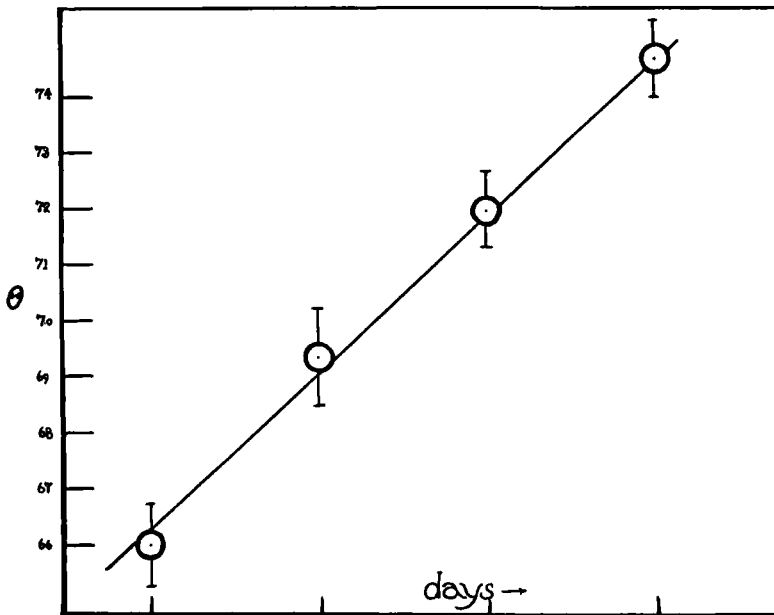


FIGURE 2

The progressive increase in the geotropic response of *Aphaenogaster fulva*. The orientation- or θ -angle measured as deviations from a line at right angles to the longitudinal axis of the plane is tested once a day on a constant inclination of 65° on an inclined plane (the α angle). Each point represents the average of 40 determinations. The short vertical lines through the points are twice the probable errors. This ant eventually died, as do most isolated individuals.

and three more days of the same treatment result in an increase to 72.8° . This individual appeared to be stronger than the one whose record is given in Figure 2.

The crucial experiment suggested by Professor Crozier was carried out with a fresh individual. This ant was kept in isolation for three days without any noticeable creeping in the watch glass. On the fourth day the geotropic angle on a 50° inclination was found to be 80.4° ! The possible effect of previous crawling on the incline or on the level was quite definitely excluded, but this ant exhibited the greatest increase in geotropic response. It is obviously important to keep in mind that these isolated individuals die if not returned to the

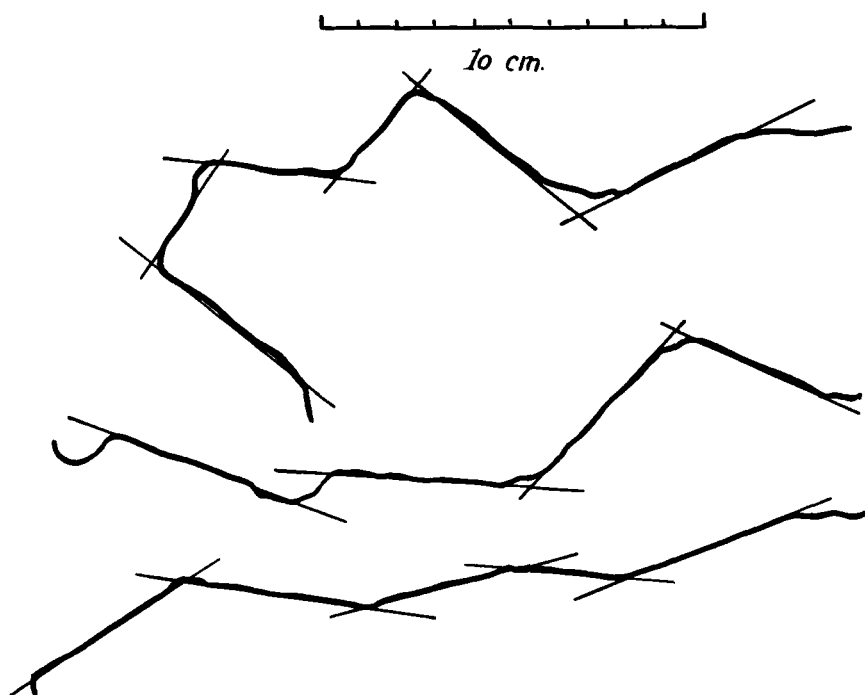


FIGURE 3

The method of measuring θ angles (of the short straight lines superimposed on the recorded path of the ant).

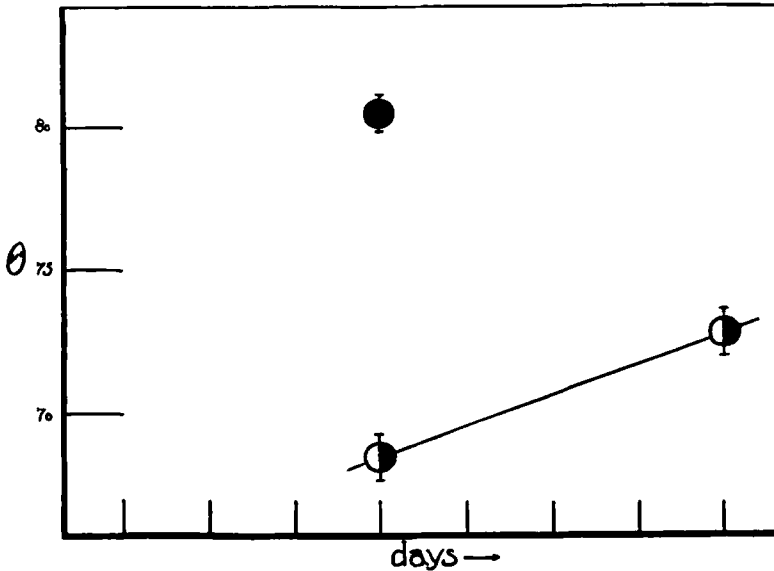


FIGURE 4

The rise of the angle of geotropic orientation with two individuals of *Aphaenogaster fulva*. The black and white points represent the rise in θ from $68.52^\circ \pm 0.79^\circ$ to $72.8^\circ \pm 0.80^\circ$ in an *Aphaenogaster* exercised on a level surface at intervals and tested on a 65° inclination. The black point is the high θ exhibited by an ant kept in isolation without crawling and then tested on a 65° slope. This value $80.45^\circ \pm 0.63^\circ$ was the highest obtained at this slope.

colony, and, after some days confinement, certain individuals tend to drop from the inclined surface at high angles. One might cautiously postulate "muscular weakness" or some irreversible change proceeding to death, but in any event our evidence proves that we are dealing with some simple physiological change. Nor must it be forgotten that a change in posture² involving a displacement of the center of gravity would influence the extent of geotropic response, for we have previously established the "muscle tension theory" of geotropism in ants.

That the asymmetry in proprioceptive stimulation produced by the

²*Aphaenogaster fulva* has unusually long legs and one frequently observes maintained changes in the orientation and degree of flexion in the legs.

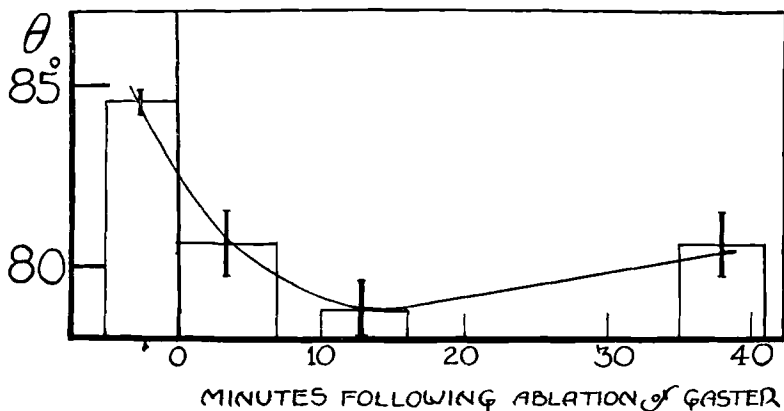


FIGURE 5

The decrease in the angle of geotropic response following ablation of the abdomen in *Aphaenogaster fulva*. $n = 40$; $\alpha = 65^\circ$.

weight of the ant on the anti-gravity muscles determines the geotropic response may be shown by ablation of the gaster. As indicated in Figure 5, the θ angle drops immediately. After a few preliminary trials the θ angle of this ant was measured at $\alpha = 65^\circ$. For each θ , 40 angles were averaged from about 10 paths each 18 centimeters long. The abdomen was then cut off and the θ value for the next series of paths became 80.6° as contrasted with 84.5° for the intact insect. In Table 3 the next four mean values are recorded, and it will be seen that the "progressive rise" in geotropic response described in the first part of this paper manifests itself again and raises the θ angle back to 84° on the second day. With *Aphaenogaster* No. 4, however, the low θ value was still exhibited 27 hours after the ablation of the gaster. With individual No. 1, whose abdomen was removed after it had given the extensive paths recorded in Table 1, a decrease of six degrees was obtained (Table 3).

Of course no ablation experiment is quite exempt from criticism, and the lower θ exhibited after the operation might follow from nervous disturbances. Although we regard this possibility as rather remote here, another method is available to demonstrate the muscle tension theory. Weights may be attached to the animal exhibiting

TABLE 3
THE EFFECT OF ABLATION OF THE GASTER ON THE ANGLE OF GEOTROPIC
ORIENTATION IN *Aphaenogaster*
 $n = 40$. The intact insect was used in Trials 1 and 9.

Trial No.	α (degrees)	θ (degrees)	P.E.	Time
<i>Aphaenogaster</i> No. 3 (negative geotropism)				
1	65	84.5 ± 0.39	Nov. 15,	3:00 P.M.
2	65	80.6 ± 0.92		3:05-3:12
3	65	78.8 ± 0.85		3:15-3:21
4	65	80.6 ± 0.92		3:43
5	65	81.6 ± 0.71	Nov. 17, 10:50-11:00 A.M.	
6	65	84.1 ± 0.61		11:05-11:14 A.M.
<i>Aphaenogaster</i> No. 4 (positive and negative)				
7	65	81.5 ± 0.90	Nov. 23, 2:48-2:55 P.M.	(27 hours after ablation)
8	65	80.9 ± 0.70		3:02-3:10 P.M.
<i>Aphaenogaster</i> No. 1 (positive geotropism)				
9	30	75.0 ± 1.13	Sept. 17, 11:16-11:19 A.M.	
10	30	68.7 ± 1.48		11:22-11:42

geotropic orientation, and the effect on the θ angle observed.³ *Aphaenogaster* No. 2 exhibited a θ angle of $69.1^\circ \pm 2.52^\circ$ on an inclination of 35° . A pupa was placed before the ant on the plane. The insect picked up the pupa in its mandibles and continued its negatively geotropic orientation but at a θ angle of $78.4 \pm 1.96^\circ$. The rise of nine degrees was produced by the weight of the pupa which, added to the worker's weight, elicited a greater proprioceptive stimulation in the supporting musculature of the latter. Each θ represents an average of 15 measurements. The rise in θ seems unusually great, and it would appear that the maintained act of gripping the pupa increased the tonus in the legs as well as in the mandibles.

The most effective way of causing a drop in the θ angle, even with individuals which exhibit the progressive rise in θ during a series of trials, is by ablation of the antennae. The path described on an inclined surface by an *Aphaenogaster* without antennae is quite sinuous and often rather erratic. The ant whose path after ablation of the antennae is recorded in Figure 6A gave a θ angle of $77.7^\circ \pm 0.92^\circ$ on an inclination of 65° to the horizontal when tested before

³Crozier and Pincus (2) showed that the angle of orientation in young rats increases about as the log of weight added at the root of the tail. In the geotropism work with rats it was not possible to test the θ angle over a period of days as with the worker ants.

the operation. The insect stopped crawling immediately after the antennae were cut off (Nov. 15, 1928, at 7 P.M.), but when placed on the plane ($\alpha = 65^\circ$) two days later (Nov. 17, 11:30 A.M.) extensive crawling was exhibited. The θ angle had fallen from $77.7 \pm .92^\circ$ to $61.1 \pm 2.09^\circ$ ($n = 40$). The amplitude of the waves in the path increased, for we found a $\frac{1}{2}\lambda$ value of 24.4 ± 1.21 mm. before ablation and $19.0 \pm .65$ mm. after the loss of the antennae ($n = 26$). The number of waves per unit length of trail is also affected,

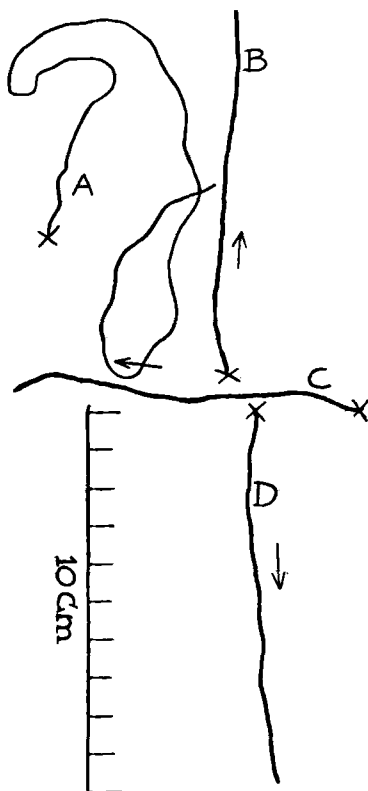


FIGURE 6

Paths described by geotropic *Aphaenogaster fulva*; all trails begin at "X."

A. Path of an ant without antennae. $\alpha = 65^\circ$.

B, C, and D. The reversal of geotropism from negative to positive in an intact *Aphaenogaster*. $\alpha = 65^\circ$.

which may be observed by measuring the distance between periodic turns or slight alternate changes in direction to right or left. Examination of 130 cm. of path in each condition showed that the intact ant moved 27.6 mm. between turns, which became 21.3 mm. (average) after ablation of the antennae. All these measurements were made with the same ant at a constant inclination of 65° to the horizontal.

The preservation of geotropic sensitivity after the loss of the antennae furnishes further support for the muscle tension theory of geotropic orientation, but our results indicate that the antennae-less insect is at least partially released from the gravitational θ -response. Perhaps the side-to-side tapping action of the antennae tends to check wide turning, as the $\frac{1}{2}\lambda$ value suggests. The ant executes balancing movements with the feelers, but it is difficult to attribute much importance to such actions from the standpoint of geotropism. It will be recalled that Wolf (5) found that antennae-less hive bees were not as greatly disturbed by rotation during transit as the intact bee. We hope to return to this unsettled point in future geotropism studies.

A reversal of geotropism occurred after the loss of the feelers in *Aphaenogaster*, from positive to negative, but such a change occurs at intervals in all geotropism records with this insect. In Figure 6, *B* represents one of 7 negative trails from an individual at $\alpha = 60^\circ$; the next 8 trails were directly to the side, *C*; and the following 4 were quite positive, *D*. This occurred in less than 10 minutes with practically continuous crawling. The sign of the response is given for all paths in the tables.

SUMMARY

Workers of the ant *Aphaenogaster fulva* exhibit a progressive increase in the extent of their geotropic response on an inclined surface. This and several other modifications of the θ angle of geotropic orientation are shown to be generated by physiological causes which may be experimentally controlled.

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Laboratory of General Psychology
Harvard University
Cambridge, Massachusetts

LA CROISSANCE PROGRESSIVE DANS LA RÉPONSE GÉOTROPIQUE DE LA FOURMI APHAENOGASTER

(Résumé)

Les ouvrees parmi les fourmis *Aphaenogaster fulva* montrent une croissance progressive dans l'étendue de leur réponse géotropique sur une surface plane. Cela et plusieurs autres modifications de θ , l'angle de l'orientation géotropique, se montrent produites par des causes physiologiques qu'on peut contrôler expérimentalement.

BARNES ET SKINNER

DIE PROGRESSIVE ZUNAHME DER GEOTROPISCHEN REAKTION BEI APHAENOGASTERAMEISEN

(Referat)

Es zeigt sich, dass bei Arbeiterameisen der *Aphaenogaster fulva* der Umfang ihrer geotropischen Reaktion auf einer schiefen Oberfläche progressiv zunimmt. Es ergibt sich, dass diese und andere Modifikationen von θ , dem Winkel der geotropischen Orientation durch physiologische Ursachen hervorgerufen werden, die experimentell geprüft werden können.

BARNES UND SKINNER